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RESEARCH ARTICLE

The impact of personality, morphotype and shore height on temperature-mediated behavioural responses in the beadlet anemone *Actinia equina*

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Abstract

1. Between-individual variation in behavioural phenotype, termed personality, is an important determinant of how populations cope with acute environmental fluctuation related to climate change.
2. Personality in the beadlet sea anemone *Actinia equina* is linked to genetically distinct morphotypes, which are associated with different heights on the shore. In the intertidal zone, high-shore environments experience more environmental fluctuation due to longer periods of exposure, and animals adapted to live in these environments are predicted to deal more effectively with environmental perturbation than their low-shore counterparts.
3. We collected beadlet anemones of two different morphotypes from three different shore heights. We investigated variation in two behaviours at three different temperatures and in a temporal control treatment where the temperature was not changed: startle response time, the time it took an anemone to re-extend its tentacles after a threatening stimulus, and immersion response time, the time to re-extend tentacles after simulated tidal immersion. These behaviours reflect risk-taking and allow individuals to be categorized as bold, shy or intermediate based upon response times.
4. Both behaviours showed significant changes as the temperature increased. For immersion response, the morphotype associated with the low-shore-lengthened response times at high temperatures. For startle response, all animals lengthened their response times at high temperatures but animals collected from the low-shore lengthened theirs to the greatest degree. At the individual level, although control individuals exhibited temporal changes in their response times, a clear effect of temperature was present in both behaviours. Shy and bold individuals became more intermediate at higher temperatures in immersion response (this effect was present to a lesser degree in control individuals), while intermediate individuals raised their response times at higher temperatures for startle response.

5. Given that prolonged tentacle retraction reduces foraging opportunities and can negatively impact respiratory efficiency, our data suggest that some individuals within a single population of *A. equina*, particularly those associated with the lower shore, may exhibit less effective behavioural responses to temperature shifts than others. These findings demonstrate that acute temperature changes influence risk-taking, and could have profound short and long-term implications for survival in the face of climate change.

KEYWORDS

behavioural plasticity, boldness, climate change, environmental history, marine invertebrate, morphotype, personality, temperature fluctuation

1 | INTRODUCTION

Anthropogenic climate change is an ever-increasing threat to global biodiversity (IPCC, 2018; Parmesan, 2006). The effects of climate change can be seen particularly in the oceans; since 1971, global average ocean surface temperatures have increased at a rate of 0.11°C per decade (IPCC, 2013), with 2018 having been the hottest year in the oceans since records began (Cheng et al., 2019). Within ocean habitats, the effects of climate change are especially apparent in intertidal zones, as they are already subject to extremely high levels of spatial and temporal heterogeneity (Brahim, Mustapha, & Marshall, 2019). Different heights on the shore vary substantially in their exposure to environmental fluctuation (Bockelmann, Bakker, Neuhaus, & Lage, 2002). This leads to highly niche-specialized intertidal flora and fauna, adapted to live at different shore heights and so under differing levels of heterogeneity in their immediate environment (Allcock, Watts, & Thorpe, 1998; Dias, Christofoletti, Kitazawa, & Jenkins, 2018). Phenotypic differences across the gradient of the shore can also extend within species, and animals adapted to certain shore heights may be more susceptible to potential environmental changes than others (Brahim et al., 2019; Chapperon et al., 2016).

An important aspect of within-species phenotypic variation is consistent behavioural differences among individuals across times and contexts (context here defined as immediate environmental conditions), also termed personality (Dall, Houston, & McNamara, 2004; Sih, Bell, & Johnson, 2004). Personality is now widely documented across a variety of taxa (Bell, Hankison, & Laskowski, 2009), including many invertebrates (Kralj-Fišer & Schuett, 2014). Aggression, exploration and risk-taking (usually referred to as boldness) are all commonly measured personality traits (Carter, Feeney, Marshall, Cowlishaw, & Heinsohn, 2013). Personality variation is linked with how individuals respond to environmental stressors both behaviourally and physiologically (Koolhaas, de Boer, Coppens, & Buwalda, 2010) and divergence in these responses to environmental challenge (e.g. Dong et al., 2008; Wong, French, & Russ, 2019) could cause varied fitness levels in the face of environmental perturbation (Killen, Adriaenssens, Marras, Claireaux, & Cooke, 2016). Investigating the effects of environmental change on personality variation can therefore contribute to our understanding of how different populations, and individuals within those populations, are likely to cope with anthropogenic climate change (Tuomainen & Candolin, 2011).

Variation in behavioural strategies to deal with different environmental conditions is becoming more widely demonstrated (Killen, Marras, Metcalfe, McKenzie, & Domenici, 2013) and personality types are often specialized to specific environments (Holtmann, Santos, Lara, & Nakagawa, 2017). In heterogeneous environments like the intertidal zone, biotic (e.g. food availability; Kolluru, Grether, & Contreras, 2007) and abiotic (e.g. temperature; Chapperon et al., 2016) selective pressures vary spatially and temporally (Araújo, Bolnick, & Layman, 2011). This can lead to these environments having a diverse range of behavioural optima, which can drive the maintenance of personality variation (Dingemanse & Wolf, 2013). Environmentally driven personality variation can extend to how different individuals plastically alter their behaviour in response to environmental fluctuations (Stamps, 2016). Where usual environmental conditions are less variable, more rigid personalities and a reduced scope for potentially energetically costly 'activational' behavioural plasticity (i.e. a rapid phenotypic shift induced by an environmental stimulus; Snell-Rood, 2013) could provide an adaptive advantage (Dall et al., 2004). Meanwhile, in stochastic environments, a lack of behavioural plasticity can be detrimental to individual fitness (Abram, Boivin, Moiroux, & Brodeur, 2017) and to the overall health of a population (van Baaren & Candolin, 2018).

Thermal variation is one of the key environmental variables being affected by climate change (Hoegh-Guldberg & Bruno, 2010; IPCC, 2018), and environmental temperature shifts can have far-reaching physiological and behavioural effects across a range of species (Abram et al., 2017; Parmesan, 2006). As a species that inhabits the intertidal zone (Allcock et al., 1998), single populations of the beadlet anemone *Actinia equina* live across wide spatiotemporal thermal gradients (Harley et al., 2006). Personality variation in *A. equina* has a known genetic component: at least three distinct morphotypes (Allcock et al., 1998), two of which are readily determined by eye, show clear differences in their boldness and aggression (Collins, Vernon, & Thomson, 2017). *Actinia equina* is

highly sedentary, and morphotypes show significant ecological distinction in their distribution across shore heights (although there is some overlap; Allcock et al., 1998). This indicates that they are adapted to live at different heights on the shore (Quicke, Donoghue, & Brace, 1983), which vary in their thermal exposure (Brahim et al., 2019). *Actinia equina* therefore provides the opportunity not only to investigate differences in temperature-mediated behavioural shifts at the level of the individual, but to further uncover how these might be linked to population-level variation brought about by environmental heterogeneity (Monteiro, Solé-Cava, & Thorpe, 1997). Those individuals of high-shore-adapted morphotypes or simply collected from higher up the shore, that experience greater environmental fluctuation with changing tides, may have increased scope for behavioural plasticity in the face of environmental shifts (Dingemanse & Wolf, 2013). This could increase their robustness to climate change-induced temperature changes (Tuomainen & Candolin, 2011), as compared with lower-shore individuals, which deal with a much more homogeneous immediate environment and should therefore be more rigid in their behaviour (Dall et al., 2004; Snell-Rood, 2013).

In this study, we measured startle response, a form of emergence test using the re-extension of feeding tentacles in recovery from a threatening stimulus (Collins et al., 2017; Lane & Briffa, 2017; Rudin & Briffa, 2012). In *A. equina*, startle response is commonly used as a proxy for boldness, since latency to recover from a disturbance can provide a measure of risk-taking (Beckmann & Biro, 2013). To investigate whether boldness in *A. equina* could be defined as an axis of behavioural variation (Carter & Feeney, 2012; Houslay & Wilson, 2017) and whether different behaviours falling on this axis might respond predictably to temperature shifts, we defined a second, potentially related behaviour: immersion response. This measurement used an anemone's latency to extend its foraging tentacles in response to simulated tidal fluctuations, which is inherently risky as it exposes tentacles to increased predation (Edmunds, Potts, Swinfen, & Waters, 1974), as opposed to recovery from a threat.

We aimed to explore underlying differences between groups (i.e. different morphotypes and shore heights) and individuals in boldness, and how these related to variation in temperature-mediated behavioural shifts. To address this, we employed a graduated temperature increase, alongside a temporal control treatment, and took repeated behavioural measures from *A. equina* individuals at each temperature, or at each equivalent timepoint for the control. Our focus was specifically on acute temperature shifts of the type that might be brought about by extreme weather events, the frequency of which are expected to increase as the climate continues to warm (IPCC, 2013). As certain behavioural responses may be more adaptively advantageous in the face of increasing temperatures than others (Abram et al., 2017; van Baaren & Candolin, 2018), we hoped to gain an understanding of which groups and personality types within a population of *A. equina* might exhibit less effective behavioural changes, and thus be particularly susceptible in future to climate change-induced acute temperature changes.

2 | MATERIALS AND METHODS

2.1 | Collection and housing

Data collection took place between April and August 2018 across four, 3-week blocks with each block randomly assigned to experimental or control treatments. Anemones were collected from the north shore of Llandudno, North Wales (lat: 53.330359, long: −3.828975). Within each block, anemones were removed from substrate using a flathead screwdriver, taking care not to cause tissue damage. A minimum of 1 m was left between each anemone collected to avoid collecting clonal individuals (Foster & Briffa, 2014). Collected anemones were split between two morphotypes which are putatively associated with different heights on the seashore (Quicke et al., 1983). Although each morphotype was far more abundant at their associated shore height, overlap in their distributions allowed sample sizes of each morphotype to be split evenly across low, mid and high-shore heights (Appendix 1.1, Table 1 in Supporting Information), which were defined by the stratification of the shore (e.g. Dias et al., 2018). The colour of the pedal disc was used to differentiate between the two morphotypes (Allcock et al., 1998). The high-shore-associated morphotype was defined as having a red or brown pedal disc (henceforth red) and the low-shore-associated morphotype was defined as having a green pedal disc (henceforth green). Where pedal disc colour was inconclusive, the presence or absence of a blue limbus around the disc was used to further differentiate the individual as green if present (Collins et al., 2017). Total sample size was 209, split between 101 (red = 65, green = 36) experimental individuals and 108 (red = 72, green = 36) controls (for a full explanation of sample sizes and associated ethical considerations, see Appendix 1.1 in Supporting Information). Upon collection, each anemone was placed into a small, sealable plastic bag filled with seawater and air. Anemones were transported to the laboratory at the University of Liverpool within 4 hr of collection. None suffered mortality and all subsequently fed.

Upon arrival to the lab, each individual was transferred into a separate 9.5 cm × 9.5 cm compartment within a larger tank (30 cm × 20 cm × 20 cm), containing a single pebble onto which they could attach. Anemones were unable to physically interact but could potentially chemically interact via the flow-through system. Tanks were filled to a depth of ~15 cm with seawater (RO Water and Tropic Marin, Germany, Pro Reef Sea Salt) and were situated on a flow-through system, located in an 18°C (±0.5°C) temperature-controlled room. Overall, 10 tanks were used to house each block of anemones, with eight tanks housing six individuals and two tanks housing three individuals (see Appendix 1.1, Figure 1 in Supporting Information for a diagram of this setup). Tanks always housed the same number of individuals across data collection blocks. The system was kept at a salinity of 34ppt (±1), a pH of 8.1 (±0.3), and was regularly monitored for water quality. Anemones were all housed at a natural baseline temperature of 11°C (±1°C; www.seatemperature.org; see Appendix 1.2 in Supporting Information). Water was chilled using an Aqua-Medic

Titan 500 chiller, and heated using an Aqua-Medic 300 W titanium heater. Animals were kept on a 12:12 hr (9 a.m. to 9 p.m.) light:dark cycle and were allowed a minimum of 2 days to acclimate to their new environment. Anemones were fed ad libitum on the final day of acclimation with Tetra Marine Flakes (Tetra GMBH) and a 50% water change was carried out before commencing behavioural trials the following day (see Appendix 1.3, Figure 1 in Supporting Information for a visualization of within-block experimental schedules).

For ease of identification, morphotypes and shore heights of anemones were standardized in each tank. This was deemed an appropriate method of housing because (a) the flow-through system allowed us to keep all experimental tanks at a uniform temperature (±1°C), and (b) the one-system setup should have meant that individuals within each data collection block were being exposed to the same chemical cues regardless of the tank they were housed in.

2.2 | Behavioural trials

2.2.1 | Timeline

Behavioural testing took place over the course of 13 days, subsequent to the initial acclimation period. In experimental treatments, anemones were initially subjected to 3 days of behavioural trials at 11°C (±1°C). Behavioural trials on each day consisted of first testing individual immersion response times (IRTs) and testing their startle response times (SRTs) 10 min after the conclusion of IRT observation. Half of the tanks were tested in the morning and half in the afternoon of each day. Tanks were randomly selected on days 1 and 3, with tanks tested in the opposite order on day 2 to ensure that all individuals experienced testing at both times of day. Within time of day the order in which tanks were subjected to behavioural trials was randomized and, for SRT trials, so was the order in which individuals were subjected to trials within tanks.

At the end of the third day of behavioural testing at 11°C (±1°C), a 50% water change was carried out and during experimental blocks the water temperature was raised to 18°C (±1°C), which is at the upper limit of what this population might experience naturally (www.seatemperature.org), overnight at a rate of 1°C per hour. Anemones were given a further 2 days to acclimate to the new temperature and once again fed ad libitum on Tetra Marine Flakes the day before behavioural trials commenced. Behavioural testing was carried out using the same process as at 11°C (±1°C) before finally repeating the process again for the last temperature of 23°C (±1°C), which was deemed near-lethal as pilot work found that anemones from Llandudno began to denature at 24–25°C.

For control treatments, the timeline of behavioural testing remained the same but the temperature stayed at 11°C (±1°C) across the 15 days. Blocks of three repeats within experimental treatments are hereafter referred to as temperatures and blocks of three repeats in controls as timepoints.

2.2.2 | Behaviour one: Immersion response time

In order to test IRT, tanks were drained by turning off the water inflow, temporarily removing the partitions separating anemones, and siphoning water directly into the system sump. This method caused minimal disturbance to animals other than the reduction in water level and took roughly 5 min per tank. Partitions were reinstated and each tank was left for 30 min before re-immersion, which was achieved by switching on the inflow. Response time was captured using time-lapse photographs, taken every 30 s, using seven Crosstour 4k (Shenzhen Longtour Optics Co. Ltd) action cameras and two GoPro Hero 4 action cameras. Each camera captured the response times of three individuals per trial. Recording began before re-immersion commenced to ensure fast responses were not missed or incorrectly measured. Fifty minutes of footage was captured for every camera, from which 45 min were used to measure IRT. We deemed 45 min an appropriate time limit as pilot work found that most individuals re-extended their tentacles within 30 min of re-immersion.

Immersion response time was defined as the length of time from when the waterline first touched the body of an individual to when an individual had fully re-extended its feeding tentacles such that the entire circumference of the collar (the upper rim of the anemone's column; Griffiths, 1977) had been surpassed and there was no longer any visible extension occurring. How many pictures a response took was recorded, and this number was multiplied by the time-lapse interval to convert values into seconds. Those individuals which did not re-extend their tentacles within 45 min were given a value of 2,700s. Photo analysis found that 5% of IRTs hit this upper bound. All behavioural values were extracted from photos by the same researcher (DKM), blinded, as far as possible given the colour differences inherent in the different morphotypes, to anemone type to avoid any inter-individual variation in results.

2.2.3 | Behaviour two: Startle response time

Startle response time was tested using a similar method to Rudin and Briffa (2012). Startle responses were elicited 10 min after the conclusion of the previous immersion trial by jetting each individual's oral disc with 50 ml of tank water from a 60-ml syringe located 1cm above an anemone, causing them to retract their tentacles. Our method differed from Rudin and Briffa (2012) in that, on time-lapse recordings, an individual's oral disc was not always visible and individuals rarely fully re-extended their tentacles. SRT was therefore defined as the time it took an anemone to re-extend its feeding tentacles such that 75% of the circumference of the collar had been surpassed. Pre-startle reference pictures were also taken, as some individuals did not have their tentacles fully extended beyond the collar at the start of trials. For these individuals, SRT was defined as the time it took for tentacles to return to their pre-startle degree of extension. Some individuals exhibited no or very limited tentacle extension at the beginning of a given trial and thus no response could be elicited. Of 1881 SRT data points, 156, spanning 89 individuals, were not quantifiable and thus excluded.

While the startle stimulus remained the same across individuals, different definitions were utilized for different datapoints as the visible behavioural response differed slightly depending on starting tentacle extension. Those individuals that began fully extended very rarely returned to their pre-startle degree of extension, even when exhibiting a large degree of recovery and returning to 'normal' behaviour. Those individuals which did not start with their tentacles fully extended, similarly, rarely began with more than 75% of their tentacles extended beyond the collar, but regularly returned to their pre-startle degree of extension. The dual definition was thus the best method to maximize sample sizes and account for the slight difference in observable responses with as accurate a measure as was feasible. There was a relatively even split of individuals between the two definitions. Re-analysing a randomly selected subset of photos from the full dataset, it was found that 62% of individuals began a given trial with their tentacles fully extended, while 38% of individuals did not. See Appendix 1.4 in Supporting Information for a full analytical justification of this.

Measurement and extraction of response times was conducted in the same way as for IRTs. In this case, cameras recorded 100 min of time-lapse footage. Each individual's SRT was measured using the 90 min of footage immediately following the syringe stimulus and those that did not exhibit re-extension within this time were given a value of 5,400s. This was deemed an appropriate upper bound, beyond which re-extension of tentacles should no longer be defined as the recovery from a threat, based on a review of SRT ranges across the current literature (e.g. Collins et al., 2017; Rudin & Briffa, 2012). Twenty-two percentage of SRT measurements reached 5,400s in this study. These values were retained for analysis as our literature review indicated that these individuals were exhibiting maximally shy behavioural responses.

2.3 | Statistical analysis

We carried out all analyses in R version 3.5.1 (R Core Team, 2018). Analysis of fixed effects on population means was carried out in lme4 (Bates, Mächler, Bolker, & Walker, 2015), using extra features from lmerTest (Kuznetsova, Brockhoff, & Christensen, 2017). All individual-level behavioural analysis followed a Bayesian Markov Chain Monte-Carlo framework, using the r package MCMCglmm (Hadfield, 2010). We ran models using both parameter-expanded and inverse-Wishart prior to ensure robustness to different specifications. Deviance information criterion (DIC, analogous to AIC values in REML analysis; Spiegelhalter, Best, & Carlin, 2002) estimates did not differ meaningfully between the two prior specifications in any model and effect estimates remained similar. Only the inverse-Wishart results are reported. Response variables were always *z*-transformed in order to improve model convergence (Houslay & Wilson, 2017). All individuals were included in all analyses, regardless of missing values, as individuals with fewer observations can still markedly improve the power of behavioural models (Martin, Nussey, Wilson, & Réale, 2011). All Bayesian models were run for 420,000 iterations with a 20,000 burn-in period and a thinning interval of 100. All models underwent full model checks; convergence and autocorrelation were checked by visual plot inspection and using both Heidelberger & Welch and Gelman-Rubin convergence tests. The significance of individual-level estimates and differences between these estimates were both determined using 95% credible intervals (e.g. Debeffe et al., 2015; Highcock & Carter, 2014; Houslay & Wilson, 2017). Bayesian models are described in brief here, but for further details of these analyses see Appendix 1.5 in Supporting Information. Graphs were drawn with ggplot2 (Wickham, 2011).

2.3.1 | Group level effects on population means

To investigate the impact of morphotype and shore height on IRT and SRT, and whether this was associated with temperature change, we ran separate univariate generalized linear mixed effects models on the full datasets (incorporating both control and experimental treatments) for each behaviour. We used stepwise model simplification to determine minimum-adequate models (MAMS). Behaviours were set as the response variable. IRT values were reciprocal root transformed to ensure model assumptions were met. Starting models contained morphotype, shore height, temperature (a three-level categorical effect in all models), time of day, data collection block and sampling occasion, which incorporated both time since feeding and time since collection, as fixed effects, and the first three were initially allowed to interact. Individual and tank were random effects. Given that tanks always housed the same number of individuals, this variable also incorporated the differing densities of anemones inherent in our housing design.

2.3.2 | Repeatability variation across temperatures and timepoints

We assessed adjusted repeatability (hereafter, repeatability) across temperatures and timepoints (hereafter, when referred to together, called contexts) by splitting experimental and control treatments into separate datasets for IRT and SRT respectively. We ran univariate mixed effects models on each dataset and extracted cross-context repeatability estimates from each (Appendix 1.5a in Supporting Information). Morphotype, shore height and sampling occasion were fixed effects, and individual was a random effect. Temperature was fitted as a further fixed effect in the experimental models and interaction terms were included in each model based on the MAMs from our REML analysis.

2.3.3 | A single axis of behavioural variation

To test whether IRT and SRT fell on the same axis of behavioural variation, we first ran a bivariate model on the whole dataset and extracted the among-individual correlation between the two behaviours (r_I; Appendix 1.5b in Supporting Information). Both IRT and SRT were set as response variables with morphotype, shore

height, temperature and sampling occasion as fixed effects and individual as a random effect. To investigate whether covariance remained stable within treatments (i.e. whether temperature change affected any correlation between the two behaviours), we ran two further bivariate models on control (with temperature no longer included as a fixed effect) and experimental datasets respectively.

2.3.4 | Within-context repeatability, between-context correlations and between-individual variation in plasticity

To examine between-individual variation in plasticity ($I \times E$) and the strength of correlations between behaviours across contexts, we utilized a character-state approach, treating each context as a separate response variable (Dingemanse, Kazem, Réale, & Wright, 2010; Houslay & Wilson, 2017). Methods of controlling for temporal variation in the laboratory typically utilize variations of crossed-over designs (e.g. Briffa, Bridger, & Biro, 2013; Mitchell & Biro, 2017) or temporal controls similar to the one employed in this study (White & Briffa, 2017) and account for time statistically. However, a unique feature of the temporal control is that it allows the direct comparison of control and experimental patterns of change by partitioning treatments into separate datasets, and that is the method utilized here. Comparison with other methods found that the character-state approach fitted these data significantly better overall (Appendix 1.5c in Supporting Information).

We specified a trivariate mixed effects model for each partitioned dataset, in which response variables were behavioural response times in each context. Morphotype, shore height and time since last feeding were specified as fixed effects and individual was specified as a random effect. We extracted repeatabilities for each response variable (i.e. repeatability within-contexts). To investigate the presence of individual differences in plasticity ($I \times E$), we calculated among-individual behavioural correlations between different combinations of contexts (Appendix 1.5d in Supporting Information).

We extracted the posterior modes of each individual's response times (analogous to BLUPs) for each context from each model to explore patterns of IxE between different contexts. Because of high levels of variance in the data, individuals were split into three starting personality types for SRT and IRT respectively ('bold', 'intermediate' and 'shy') based on the mean of their predicted values in the first context. Equivalent mean values for the other contexts were extracted for each personality type. The magnitude of changes in predicted response times for each personality type between contexts was calculated (Appendix 1.5e in Supporting Information).

3 | RESULTS

3.1 | Temperature and group-level effects

Temperature interacted with morphotype ($F = 16.26_{1,1126}$, $p < 0.001$) but not shore height to impact the length of IRTs. This effect was small in the context of the overall range of individual within-context means (130s–2,110s; Appendix 1.6 in Supporting Information) but was still clear and significant. The higher-shore-associated red morph shortened IRTs at 18°C (becoming bolder). The lower-shore-associated green morph lengthened IRTs at 23°C, such that red individuals exhibited shorter IRTs than their green counterparts at that temperature. Temperature interacted with shore height ($F = 10.68_{2,1703}$, $p < 0.001$) but not morphotype for SRT. Individuals from the low shore lengthened SRTs at 18°C (becoming shyer) while those from the mid and high shore did not. At 23°C mid and high shore individuals also lengthened their SRTs, but low-shore individuals still exhibited the longest response times. SRTs further differed between morphotypes ($F = 8.91_{1,198}$, $p = 0.003$), but this difference was independent of temperature. Green morphotypes exhibited consistently shorter SRTs than red morphotypes across all temperatures. Sampling occasion explained a significant amount of variance in both models (IRT: $F = 4.72_{8,1683}$, $p < 0.001$; SRT: $F = 10.18_{8,1528}$, $p < 0.001$).

These data show that those anemones living lower down the shore, or of the lower-shore-associated green morphotype, altered their behaviour differently at high temperatures than their higher-shore-associated counterparts. Figure 1 provides a visualization of the effects of morphotype and shore height for each behaviour in control and experimental treatments.

3.2 | Repeatability across contexts

Significant across-context repeatability was observed for SRT and IRT in both experimental (SRT: $R = 0.45$, 95% CI = 0.35, 0.55; IRT: $R = 0.21$, 95% CI = 0.13, 0.29) and control (SRT: $R = 0.43$, 95% CI = 0.33, 0.53; IRT: $R = 0.19$, 95% CI = 0.12, 0.27) treatments. Models containing an individual intercept term fit the data significantly better than models where this was removed for both SRT (Experimental With: DIC = 1,956; Experimental Without: DIC = 2,354; Control With: DIC = 2,092; Control Without: DIC = 2,454) and IRT (Experimental With: DIC = 2,444; Experimental Without: DIC = 2,567; Control With: DIC = 2,626; Control Without: DIC = 2,742), further indicating significant repeatability in both behaviours. Very similar estimates and strongly overlapping 95% credible intervals suggest that across-context repeatability in both behaviours was not significantly affected by temperature change. These results are indicative of personality and show that between-individual differences were maintained to the same degree in the presence and absence of a graduated temperature increase.

3.3 | A single axis of behavioural variation

Bivariate models show significant between-individual correlations between IRT and SRT across the whole dataset ($r_I = 0.55$, 95% CI = 0.40, 0.69). Correlation coefficients remained stable for control data ($r_I = 0.55$, 95% CI = 0.37, 0.74) but were reduced in the

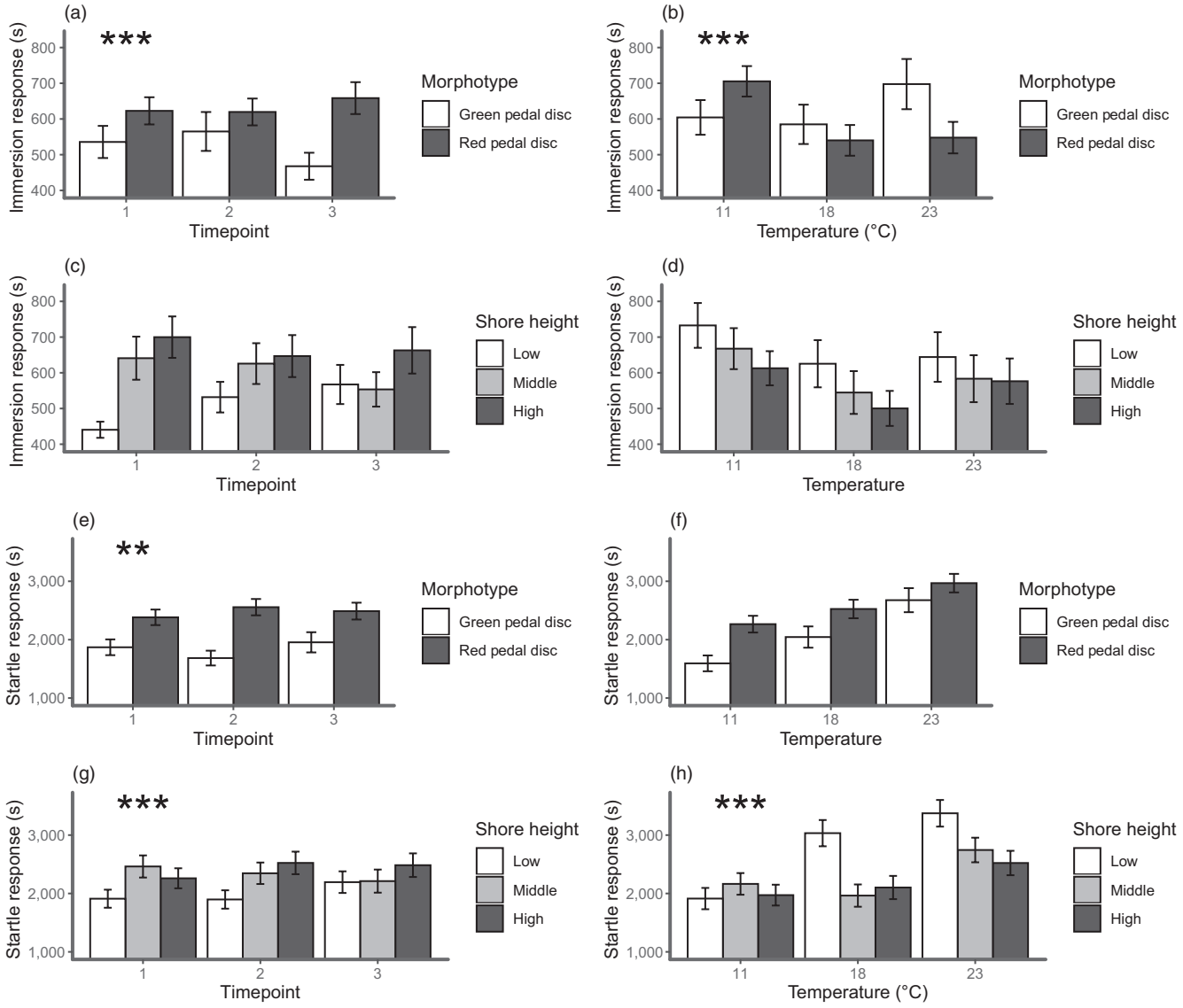

FIGURE 1 Variation in mean immersion and startle response times, across timepoints for 108 control beadlet anemones (panes a, c, e and g) and temperatures for 101 experimental anemones (panes b, d, f and h), for different morphotypes/shore heights. Means are derived from three repeated measures per anemone within each timepoint/temperature. Significance of single morphotype/shore height terms, determined from generalized linear mixed effects models, is denoted by asterisks above control plots. Significant interactions between morphotype/shore height and temperature are denoted by asterisks above experimental plots. $p < 0.01$ is denoted by '**', $p < 0.001$ is denoted by '***'

experimental dataset ($r_I = 0.40$, 95% CI = 0.19, 0.64). These correlations show that a statistically significant portion of the between-individual differences in these behaviours fell on a single axis of variation. This axis could plausibly be defined as a 'boldness–shyness' continuum, with faster responders in both behaviours being 'bolder' (i.e. less risk-averse or more risk-prone). For the full and control datasets, correlation coefficients were moderate ($r_I = 0.55$), indicating that variation in one or both behaviours that was not explained by this axis was also present. The relationship decoupled to some extent when individuals were subjected to increasing temperatures ($r_I = 0.40$), indicating that patterns of temperature-related between-individual variation in plasticity ($I \times E$) may have differed between these behaviours.

3.4 | Repeatability within contexts

Repeatability estimates derived from character-state analyses remained significant within contexts for both experimental and control treatments (Table 1). IRT and SRT were more repeatable across short timeframes of 3 days, as within-context estimates were uniformly higher than across-context estimates derived from nine repeated measures taken over 13 days. Although some fluctuations in within-context estimates both between treatments and between contexts were present, estimates within each behaviour remained broadly similar. These similarities, coupled with highly overlapping 95% credible intervals (Table 1), indicate that no firm conclusions should be drawn concerning these differences (see Bierbach, Laskowski, & Wolf, 2017).

Behaviour	Treatment	Timepoint	Temperature	Adjusted *R*	95% CI
IRT	C	1	11	0.34	0.24, 0.45
		2	11	0.26	0.17, 0.36
		3	11	0.28	0.18, 0.37
	E	1	11	0.38	0.27, 0.5
		2	18	0.32	0.23, 0.44
		3	23	0.32	0.21, 0.43
SRT	C	1	11	0.5	0.4, 0.61
		2	11	0.55	0.45, 0.65
		3	11	0.59	0.49, 0.69
	E	1	11	0.61	0.52, 0.72
		2	18	0.66	0.57, 0.75
		3	23	0.58	0.48, 0.68

TABLE 1 Adjusted repeatabilities (*R*), explaining the variation in behaviour attributable to between-individual differences, within timepoints for control treatments and temperatures for experimental treatments for immersion response time (IRT) and startle response time (SRT), alongside associated 95% credible intervals for control (C) and experimental groups (E). Repeatabilities were extracted from trivariate Bayesian GLMMs utilizing a character-state approach and are derived from three repeated measures per individual beadlet anemone within each timepoint/temperature

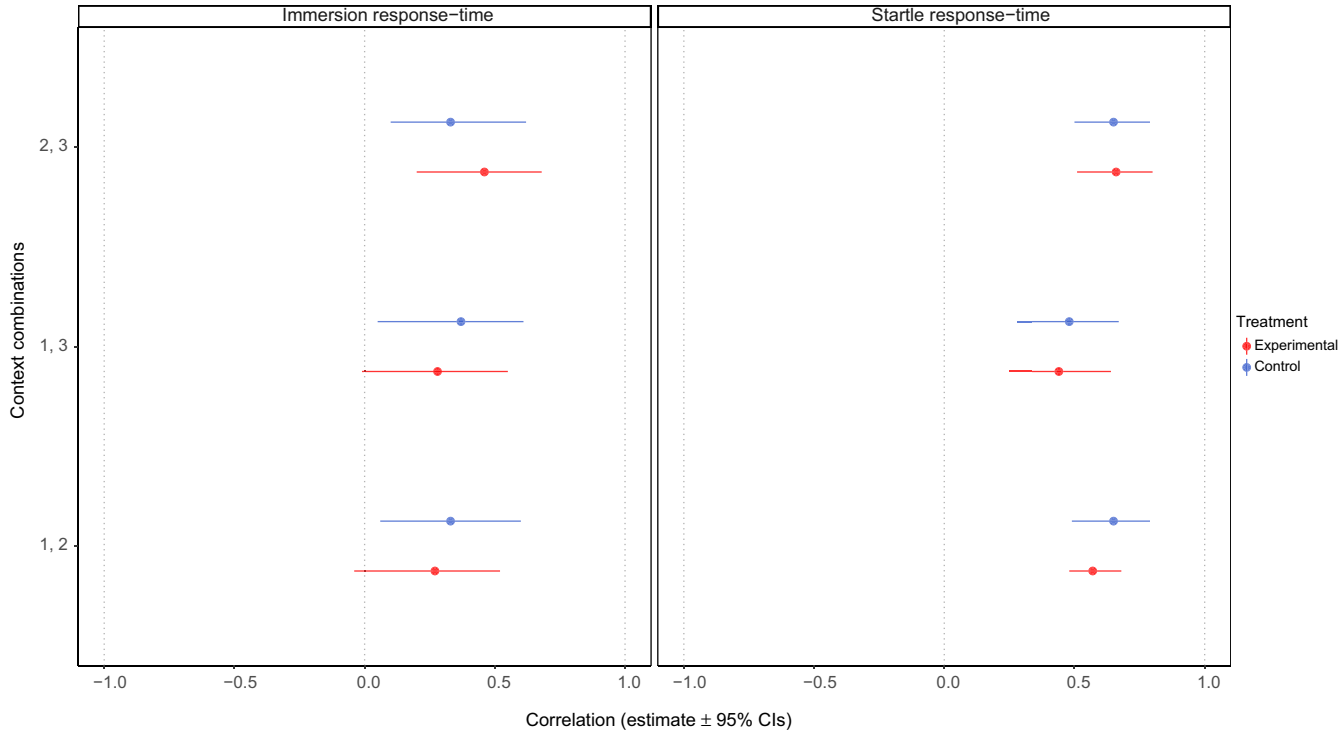

FIGURE 2 Correlation coefficients and associated 95% credible intervals between behaviours in across different combinations of contexts, extracted from the posterior covariance structures of trivariate Bayesian GLMMs, for immersion response time (IRT; left panel) and startle response time (SRT; right panel). For experimental treatments contexts denote different temperatures (1 = 11°C, 2 = 18°C, 3 = 23°C) and for controls, contexts denote the same numbered timepoint

3.5 | Between-individual variation in plasticity and correlations between contexts

For IRT, $I \times E$ was present in both treatments. Correlations remained steady and significant between different timepoints in controls (Figure 2) and were relatively weak, consistent with relatively low across-context repeatability estimates. In experimental treatments, although there was clear overlap with the 95% CIs of control estimates, the patterns of cross-context correlation were markedly different (Figure 3). Coefficients were reduced and non-significant, indicating no significant repeatability, between 11°C and both higher temperatures (Figure 2) whilst increasing and becoming significant, indicating higher repeatability, between 18 and 23°C (Figure 2). Looking at patterns of change, a temporal effect was again present in control treatments (Figure 3). Here, both bold and shy individuals moved away from personality extremes, with bold individuals lengthening response times and shy individuals shortening theirs, between the first and second timepoints. Intermediate individuals did not alter their behaviour. This effect was also present in experimental treatments (Figure 3), but the magnitude of changes for

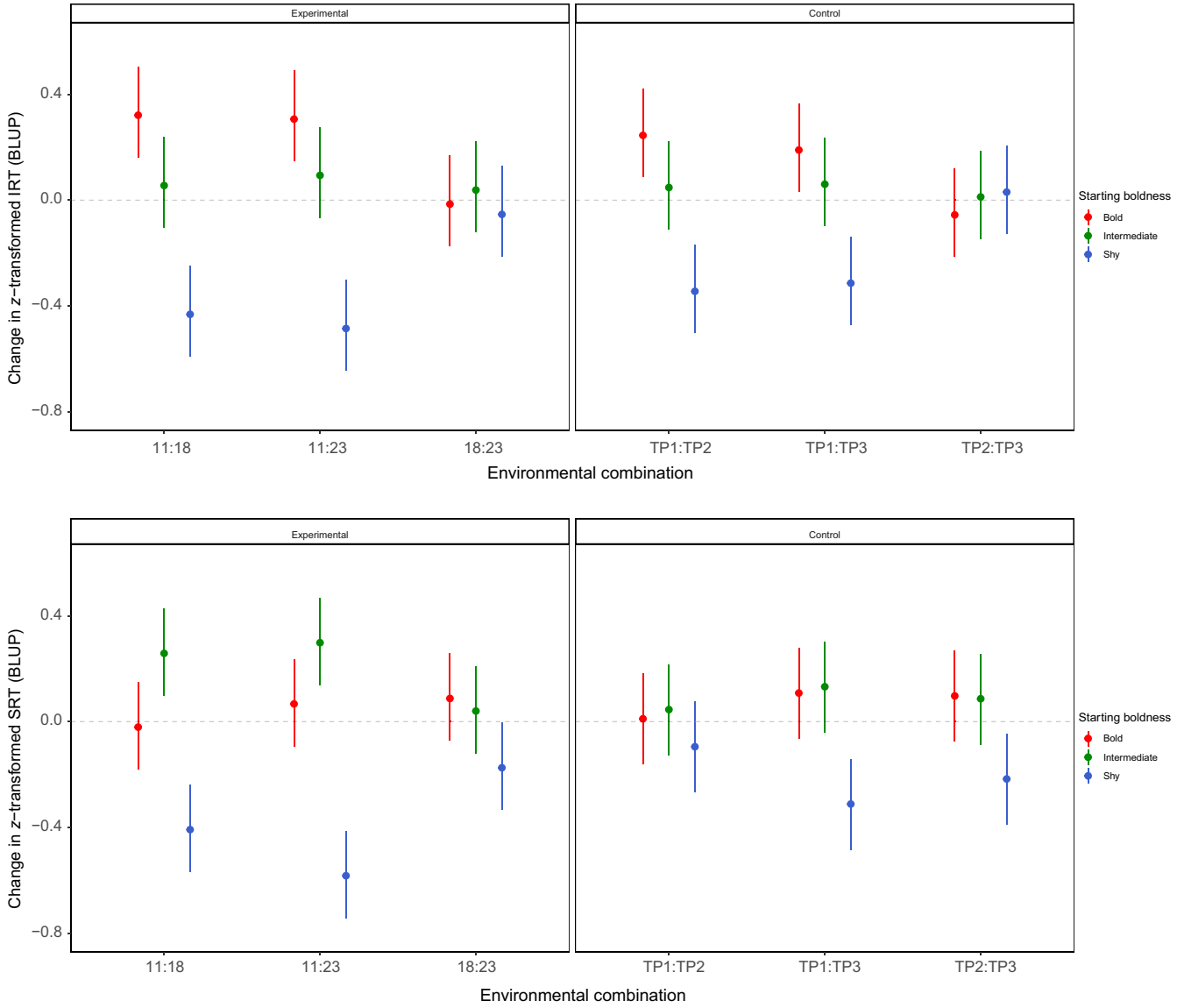

FIGURE 3 The magnitude of change in the mean of the Bayesian BLUPs extracted from trivariate GLMMs for immersion response times (IRTs; top panels) and startle response times (SRTs; bottom panels) and their associated 95% credible intervals across different combinations of temperatures for experimental treatments (left panels) or timepoints for control treatments (right panels). Different colours denote different personality types of *Actinia equina* (based on response times at 11°C or timepoint one). Changes were deemed to be significant where 95% credible intervals did not cross zero, with negative changes indicating individuals becoming bolder and shortening their response times, and positive changes indicating individuals becoming shyer and lengthening their response times

both bold and shy individuals was greater (although again note some overlap in 95% CIs). These results indicate high temporal variability in IRTs, but also show differences between individuals in how they altered their IRT in response to temperature change. Bold and shy anemones became more intermediate in their IRTs when the temperature was increased than they did over time alone.

Correlations between contexts also reveal further evidence for $I \times E$ in SRT for both control and experimental treatments (Figure 2). Coefficients in the two treatments were similar, but investigating patterns of change shows that temperature, as well as time, had an effect at the individual level. Predicted response times in control treatments show shy individuals shortening their response times and thus becoming bolder over time (Figure 3). Changes in experimental treatments differed from those in controls and unlike the equivalent control timepoints, the majority of these changes occurred between 11 and 18°C. Shy individuals shortened their SRTs to a greater degree than in control treatments, and intermediate individuals lengthened theirs (Figure 3). Intermediate individuals only showed significant levels of plasticity in experimental treatments, while shy individuals showed significantly shorter SRTs over time in both treatments (Figure 3). These data show that temporal variation was an important factor in determining individual-level changes in SRT, but that increasing temperatures affected how shy and intermediate individuals

altered their SRTs across contexts. The SRTs of the boldest individuals remained stable in both treatments.

4 | DISCUSSION

Temperature fluctuations due to climate change are predicted to increase extreme weather events such as heat waves (IPCC, 2013). This could have detrimental and wide-ranging effects on organisms in their natural environment. By simulating this, our findings demonstrate that a potentially stressful temperature increase significantly affected risk-related behaviour in *A. equina*. We found consistent, mean-level behavioural differences between individuals and between groups (i.e. morphotypes and shore heights). Overall repeatabilities in SRTs were consistent with estimates from recent studies of *A. equina* (e.g. Osborn & Briffa, 2017). These analyses also revealed a second repeatable behaviour in this species, in the form of IRT. A moderate 'boldness–shyness' continuum explaining variation in both behaviours did appear to be present and this decoupled to some degree in experimental treatments. We further quantified much of the variation inherent in the individual-level behavioural effects of environmental change ($I \times E$). By investigating cross-context repeatabilities we found that individual consistency was not clearly affected by temperature. Cross-context correlations and inspection of patterns, however, showed that at both the group and between-individual levels SRT and IRT exhibited temperature-dependent change, the patterns of which differed between behaviours.

The different patterns observed for SRT and IRT suggest that temperature responses in these behaviours should be considered separately. While significant correlations between them indicate that a 'boldness–shyness' continuum is present, moderate coefficients suggest that one or both behaviours may also fall on other behavioural axes. The explanatory importance of the relationship between these two behaviours may be further reduced as the temperature is increased, leading the axis to decouple and each behaviour to exhibit different patterns of temperature-related change. This suggests that the mechanistic underpinnings of these behaviours may differ and that the relevance of the relationship between them in terms of their temperature-related plasticity may be limited. These behaviours do reflect different demands made upon the animal. SRT indicates recovery from a threat, while IRT is indicative of the natural response to the cessation of air emersion, leading to the resumption of feeding and optimal respiration (Navarro, Ortega, & Madariaga, 1981).

In IRTs, temperature-related change at the group level might be attributable to increasing metabolic demand (Abram et al., 2017; van Baaren & Candolin, 2018). While we did not measure metabolic rate in the present study, it has been shown to increase with ambient temperature in *A. equina*, with specific metabolic responses varying depending on an individual's environmental history (Navarro et al., 1981). In ectotherms, when metabolic rate increases individuals tend to exhibit faster behaviours to keep up with increased energetic costs (Abram et al., 2017). The expected pattern should have been for all individuals to re-extend their tentacles more quickly, shortening response times, as the temperature rose, enhancing oxygen uptake and allowing foraging to meet metabolic demands. Although the green morphotype showed shorter (bolder) IRTs at 11°C, red morphotypes shortened response times to similar levels as their green counterparts at 18°C, indicating enhanced metabolic demand. The green morphotype, associated with the low shore and thus likely to be less well adapted to dealing with temperature fluctuation (Quicke et al., 1983), showed no similar reduction and exhibited possibly maladaptive longer IRTs at 23°C. Differing behavioural thermal performance curves, whereby individuals quicken their behaviours up to a thermal maximum beyond which they can no longer effectively mediate them, could explain the discrepancy between morphotypes (Abram et al., 2017). It is possible that individuals of the green morphotype had surpassed their critical temperature at 23°C. Red individuals meanwhile, whose IRTs remained stable between 18 and 23°C, may retain mechanisms to mediate their IRTs even when temperatures near potentially lethal levels.

At the between-individual level, high levels of within-individual behavioural variation (Stamps, Briffa, & Biro, 2012) may have been a factor in apparent time-related change in control IRTs, as between-individual correlations across contexts were low but remained uniform (see Dingemanse et al., 2010). This would be consistent with the relatively low estimate of between-timepoint repeatability in this behaviour. Thermal stress, meanwhile, could have caused individuals to perform larger, more varied behavioural changes between 11 and 18°C than the equivalent control timepoints, indicated by lower across-context correlations, and led to more consistency and thus a higher across-context correlation between 18 and 23°C. When grouped based on personality type, both shy and bold control individuals became less extreme in their average IRTs between the first and second timepoint. This could again indicate high levels of intra-individual variation, causing the IRTs of initially bold or shy individuals to appear more intermediate over longer timeframes. Patterns under temperature change retained this indication of high within-individual variation between 11 and 18°C but, when coupled with higher cross-context correlations between 18 and 23°C, suggest that within-individual and population-level variance may have been reduced at higher temperatures. Increased metabolic demand could feasibly reduce the adaptive scope for variability in behaviours directly related to metabolism (e.g. Velasque & Briffa, 2016) but this is in contrast to within-temperature repeatability estimates, which provide no indication that the consistency of IRTs increased with temperature. Although these estimates are based on fewer repeated measures than the across-context correlations and would thus be less likely to reveal specific patterns, future studies would be well-served to investigate this further. Understanding temperature-dependent changes in both metabolic rate and intra-individual variation will be crucial to determining whether patterns in IRT are indeed driven by metabolic changes, and whether this leads to increased stability of IRTs at higher temperatures.

In contrast to IRTs, all groups lengthened their SRTs as the temperature increased, indicating that temperature response in this behaviour was unlikely to have been solely driven by metabolic changes

(Abram et al., 2017). Green individuals were bolder, showing shorter SRTs, at all temperatures but anemones from the low shore lengthened their SRTs to a much greater degree at higher temperatures than their conspecifics from other shore heights. Low-shore individuals, which are immersed for longer periods of the day, may have more environmental scope to up-regulate this response. They may also be less acclimated to temperature fluctuations (Chapperon et al., 2016) and therefore be more stressed at high temperatures (Abram et al., 2017), leading them to be more risk-averse or physiologically unprepared in the face of further stressors (Koolhaas et al., 2010; Wong et al., 2019).

Varied temperature responses further extended to different personality types for SRTs. Shy individuals followed a common pattern of habituation in control treatments where they became bolder upon repeated exposures to a stressor (e.g. Edwards, Winney, Schroeder, & Dugdale, 2013; Houslay, Earley, Young, & Wilson, 2019). When the temperature was changed, different personality types exhibited different behavioural responses. Shy individuals became bolder by shortening their response times to a greater degree than in control treatments, and the overall population-level trend to lengthen SRTs at higher temperatures may have been driven by intermediate individuals, which only exhibited significant plastic changes in experimental treatments. The stability of bold individuals in both treatments could indicate that they have less scope for plasticity in SRTs (e.g. Kareklas, Arnott, Elwood, & Holland, 2016). Differences between personality types in their degree and pattern of temperature-related SRT change could suggest varied molecular 'coping styles', where different personality types exhibit different molecular and, in turn, behavioural responses to stress (Koolhaas et al., 2010; Wong et al., 2019). Although this phenomenon is well known in vertebrates (e.g. Pusch, Bentz, Becker, & Navara, 2018; Thomson, Watts, Pottinger, & Sneddon, 2011), the links between behavioural plasticity and molecular changes in invertebrates are poorly understood (Fürtbauer, 2015) and further work will be required to uncover the potential physiological basis of plasticity in SRTs. From an ecological perspective, these patterns of plasticity could come at a detriment to the survival of some groups, as they may be placed under increased metabolic stress whenever responding to threats at higher temperatures (Griffiths, 1977; Sebens, 1981). Intermediate personality types living lower down the shore may be particularly poorly equipped to mediate their SRTs under climate change-induced heat waves.

There has been increased call for conservation strategies to move beyond population-based approaches in the conservation of marine systems being exposed to environmental change (Brooker et al., 2016; Killen et al., 2016). These laboratory results indicate that more effective and targeted strategies might indeed be designed by considering finer-scale variation. Both behaviours are ecologically relevant and although SRT changes in relation to temperature may not be solely predicated on metabolic demand, elevated periods of tentacle retraction, especially at higher temperatures, still come at a metabolic cost (Griffiths, 1977; Sebens, 1981). Both behaviours would thus be important when considering the survival of this species in the face of climate change-induced heat waves. When designing conservation strategies in heterogeneous environments, multi-faceted investigations of multiple behaviours (Carter & Feeney, 2012) are likely to provide indications of which individuals of a given species will be more vulnerable to acute, climate change-induced temperature shifts (see Sih, Cote, Evans, Fogarty, & Pruitt, 2012).

5 | CONCLUSIONS

Acute, extreme temperature shifts associated with anthropogenic climate change could have significant effects on populations living in the intertidal zone. We show that morphotype, shore height and individual-level variation all affect behavioural responses to temperature change in *A. equina*. The highly complex relationship between behaviour and temperature in this species highlights the importance of incorporating multi-faceted behavioural approaches when designing strategies to predict the effects of anthropogenic climate change in these environments. A failure to target the most vulnerable groups or individuals in intertidal populations could lead to a loss of genetic diversity, leaving populations potentially more susceptible to future short-term and longer-term environmental perturbation.

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AUTHORS' CONTRIBUTIONS

D.K.M., J.S.T., L.U.S. and K.E.A. designed and formulated the study; D.K.M., D.C.C.W., J.S.T. and L.U.S. all contributed to the setup of laboratory apparatus; D.K.M. carried out all laboratory experiments with assistance from D.C.C.W. All authors contributed extensively during the formulation of the manuscript.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.rn8pk0p6x (Maskrey et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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